Ecology, 100(7), 2019, e02698

Interspecific prey neighborhoods shape risk of predation in a savanna ecosystem

Caroline C. Ng'weno ,[1,2] Adam T. Ford,[3] Alfred K. Kibungei, [2] and Jacob R. Goheen[1,4]

[1]*Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA*
[2]*Conservation Department, Ol Pejeta Conservancy, Private Bag-10400, Nanyuki, Kenya*
[3]*Department of Biology, University of British Columbia, Kelowna, British Columbia V6T 1Z4 Canada*

Citation: Ng'weno, C. C., A. T. Ford, A. K. Kibungei, and J. R. Goheen. 2019. Interspecific prey neighborhoods shape risk of predation in a savanna ecosystem. Ecology 100(7):e02698. 10.1002/ecy.2698

Abstract. The vulnerability of an individual to predation depends on the availability of other prey items in the surrounding environment. Interspecific prey aggregations or "neighborhoods" may therefore affect an individual's vulnerability to predation. We examined the influence of prey neighborhood structure (i.e., the densities and identities of prey neighborhoods) on spatial variation in predation in a multi-prey system with a primary apex predator. We combined GPS locations of lions (*Panthera leo*), kill-site surveys, and spatially explicit density estimates of five species of ungulates for which a significant level of predation was attributable to lions. In addition to the dual influence of predator activity and vegetation, predation risk was attributable to the structure of prey neighborhoods for at least two of the five species of prey. Along with traditionally recognized components of predation (the rate of predator–prey encounters and prey catchability), we encourage ecologists to consider how prey neighborhood structure influences spatial variation in predation risk.

Key words: associational refuge; associational susceptibility; consumer–resource dynamics; functional response; lion; predation risk; prey catchability; prey encounter; short-term apparent competition; ungulate.

Introduction

Predation is one of nature's greatest biological forces, altering the abundance and behavior of prey, sometimes with cascading effects for community structure and ecosystem function (Paine 1966, Peckarsky et al. 2008, Hawlena and Schmitz 2010, Breviglieri et al. 2017; Morris and Letnic 2017). Central to our understanding of predator–prey interactions is the heterogeneous distribution of prey, in which prey aggregations are assumed to confer net fitness benefits that exceed the costs of a gregarious lifestyle (Pulliam and Caraco 1984, Stensland et al. 2003, Sridhar et al. 2009). The benefits of prey aggregation include heightened vigilance and detection of predators (Hunter and Skinner 1998, Ward et al. 2011), predator confusion (Olson et al. 2013), collective defense (Bertram 1978, Krause and Ruxton 2002), and risk dilution (Hamilton 1971, Dehn 1990, Caro and Girling 2005, Schmitt et al. 2014). The costs of prey aggregation include greater potential for resource competition and disease transmission (Sinclair 1985, Craft 2015).

The costs and benefits of prey aggregations have been examined largely through the lens of single-species aggregations, which have examined optimal sizes and shapes of aggregations to provide safety, reduce vigilance, and maximize foraging rates (Hamilton 1971, Lehtonen and Jaatinen 2016). In addition to single-species aggregations, there is some research suggesting that larger-scale, multi-species aggregations (hereafter called prey "neighborhoods," aggregations of multiple species of prey in the same home range of the predator; sensu Addicott et al. 1987) also could change species-specific vulnerability of individuals to predation (Stensland et al. 2003, Goodale et al. 2017). For example, sticklebacks (*Culaea inconstans*) and minnows (*Pimephales promelas*) often occur together in streams and have a shared predator (i.e., yellow perch [*Perca flavescens*]). Because sticklebacks reduce their risk of predation with bony, protective plates, minnows prefer to associate with conspecifics over sticklebacks, whereas sticklebacks preferentially associate with minnows when predation risk is high (Mathis and Chivers 2003). Similarly, Grant's gazelle (*Nanger granti*) reduce risk of cheetah predation by associating with smaller and more vulnerable Thomson's gazelles (*Eudorcas thomsonii*; Fitzgibbon 1990), and predation risk to zebra (*Equus burchelli*) is lower in association with wildebeest (*Connochaetes taurinus*; Sinclair 1985). Collectively, these studies suggest that benefits of aggregation may not be shared equally among individuals from different species co-occurring in the same area.

Manuscript received 28 September 2018; revised 30 January 2019; accepted 20 February 2019. Corresponding Editor: Madan K. Oli.

[4] Corresponding Author. E-mail: jgoheen@uwyo.edu

The study of large mammals in African savannas has generated a deep body of empirical and theoretical work on predator–prey interactions. Over the past decade, several influential studies have attempted to distinguish when predators attempt to maximize encounters by hunting where prey are most abundant (the probability of a predator encountering prey) from where prey are most catchable (the probability of a successful attack, given an encounter with prey; Hopcraft et al. 2005, Valeix et al. 2009*a*, Thaker et al. 2011, Davies et al. 2016). In spite of this work, the influence of prey neighborhoods on predation risk remains largely unexplored (see Hebblewhite et al. 2005, Atwood et al. 2009, Gervasi et al. 2013 for examples from northern latitudes). This knowledge gap arises because the constituent species in a prey neighborhood frequently vary in traits that affect their vulnerability (Creel et al. 2014, Schmitt et al. 2014). Both the density and the traits of species in a prey neighborhood could alter vulnerability to predation for individual prey if, for example, smaller species are at greater risk of predation than larger species (Sinclair et al. 2003, Hopcraft et al. 2010).

We examined the effect of prey neighborhood structure alongside the effects of two commonly considered "components" of predation (Lima and Dill 1990, Moll et al. 2017), predator–prey encounter rates and catchability (the probability of a kill given an encounter, sensu Hopcraft et al. 2005, Ford et al. 2014), on patterns of mortality from predation for a multi-prey system in a semiarid savanna. Here, we equate "prey neighborhood structure" as the density and identity of prey species in the vicinity of a kill site. This definition includes conspecifics and heterospecifics, but excludes species unlikely to be killed by the focal predator. We tested three groups of hypotheses to explain the location and species identity of kills made by lions: (1) the Prey Neighborhood Hypothesis, (2) the Prey Catchability Hypothesis, and (3) the Predator–Prey Encounter Hypothesis, in addition to interactions among 1–3.

With regard to the Prey Neighborhood Hypothesis, we tested three subhypotheses representing different prey neighborhood structures. These subhypotheses are not an exhaustive set of prey neighborhood possibilities; rather, they reflect a compromise between our a priori understanding of this system and analytical tractability (Burnham and Anderson 2002).

Hypothesis 1A. Prey Neighborhood: conspecific density.—Vulnerability to predation for a focal species is a function of conspecific density, such that risk of predation (Ford et al. 2014, Ali et al. 2017) is diluted with increasing density of conspecifics.

Hypothesis 1B. Prey Neighborhood: total prey density.—Vulnerability to predation for a focal species is a function of the total density of prey in the neighborhood, such that the combined density of conspecifics and heterospecifics—but not their identity—influences risk of predation (Fortin and Fortin 2009).

Hypothesis 1C. Prey Neighborhood: zebra density.—Zebra are the most abundant wild ungulate in our study system, where they support a population of recently recolonized lions (Frank et al. 2003, Georgiadis et al. 2007). The distribution and abundance of such numerically dominant prey should be particularly influential with regard to consumption of rarer (secondary) prey (Root 1973). If hunting by predators is targeted toward areas with high cumulative prey availability, secondary prey that occur in close proximity with primary prey should face rates of predation higher than expected based on their abundance (Stephens and Krebs 1986, Schmidt et al. 2001). Likewise, secondary prey should face low rates of predation relative to their abundance when they occur away from concentrations of their primary prey. Therefore, given the prevalence of zebra in lion diets (see *Materials and Methods: Densities, resource selection, and predation risk for lion prey*), and the tendency for lions to concentrate their hunting activity in areas where zebra are abundant (Ng'weno 2017), we expected vulnerability to predation for a (non-zebra) focal species to be particularly influenced by its spatial association with zebra. On the one hand, vulnerability to predation for a larger-bodied focal species could be diluted through association with zebra (i.e., associational refugia), which may be more vulnerable to predation (Sinclair et al. 2003, Whelan et al. 2003, Owen-Smith and Mills 2008, Hopcraft et al. 2010, Preisser and Orrock 2012). Alternatively, vulnerability to predation for a smaller-bodied focal species could be enhanced through association with zebra (i.e., associational susceptibility or short-term apparent competition), which may be less vulnerable to predation (Holt and Kotler 1987, Brown and Mitchell 1989, Sinclair et al. 2003, Owen-Smith and Mills 2008, Hopcraft et al. 2010, Preisser and Orrock 2012).

Additionally, we tested the following hypotheses.

Hypothesis 2. Prey Catchability.—Vulnerability to predation for a focal species changes in areas with vegetative cover (Hopcraft et al. 2005, Thaker et al. 2011, Valeix et al. 2011, Loarie et al. 2013, Ford et al. 2014) regardless of conspecific or heterospecific density.

Hypothesis 3. Predator–Prey Encounters.—Vulnerability to predation for a focal species is correlated positively with lion activity (Fischhoff et al. 2007, Thaker et al. 2011), regardless of conspecific or heterospecific density.

Finally, we tested for plausible two-way interactions and a three-way interaction between Hypotheses 1, 2, and 3.

Hypothesis 1 × Hypothesis 2. Prey Neighborhoods × Prey Catchability.—Vulnerability to predation for a focal species changes in areas with high vegetative cover, contingent on conspecific density, total prey density, or zebra density.

Hypothesis 1 × Hypothesis 3. Prey Neighborhoods × Predator–Prey Encounters.—Vulnerability to predation for a focal species is correlated positively with lion activity, contingent on conspecific density, heterospecific density, or zebra density.

Hypothesis 2 × Hypothesis 3. Prey Catchability × Predator–Prey Encounters.—Vulnerability to predation for a focal species arises from a combination of lion activity and vegetative cover (Tambling et al. 2010, Loarie et al. 2013), regardless conspecific density, heterospecific density, or zebra density.

Hypothesis 1 × Hypothesis 2 × Hypothesis 3. Prey Neighborhoods × Prey Catchability × Predator–Prey Encounters.—Vulnerability to predation for a focal species changes in areas with high vegetative cover, contingent on lion activity and conspecific density, heterospecific density, or zebra density.

Materials and Methods

Study area

We conducted our study at Ol Pejeta Conservancy, a 364-km^2 semiarid savanna (0°.00′ N–0°.02′ S; 36°.44′–36°.59′ E) in Laikipia County, Kenya. Mean annual rainfall across the property is 900 mm, with marked interannual variation (Birkett 2002, Wahungu et al. 2011). Ol Pejeta is characterized by a discontinuous overstory of *Acacia drepanolobium* and *Euclea divinorium*; the property is managed jointly for wildlife conservation and cattle (*Bos indicus*) production. Approximately 70 lions occur in five prides and are responsible for a significant level of predation on the most common large (≥30 kg) ungulates, which account for 78% of the large ungulates on Ol Pejeta: buffalo (*Syncerus caffer*), hartebeest (*Alcephalus busephalus*), impala (*Aepyceros melampus*), warthog (*Phacochoerus aethiopicus*), and plains zebra (hereafter simply "zebra"; Appendix S1: Fig. S1). Other large carnivores include African wild dogs (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), leopards (*Panthera pardus*), and spotted hyena (*Crocuta crocuta*). In addition to the aforementioned species, less-common ungulates at Ol Pejeta Conservancy include black (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*), eland (*Tragelaphus oryx*), elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), Grant's gazelle, Grevy's zebra (*Equus grevyi*), oryx (*Oryx beisa*), Thomson's gazelle, and waterbuck (*Kobus ellipsiprymnus*).

Lion capture and kill site surveys

Between March and May 2014, and with the assistance of a Kenya Wildlife Service veterinary team, we captured and immobilized five female lions from different prides representing 55 individuals (see methods in Frank et al. 2003). Lions were darted using a CO_2 rifle (Dan-inject RSA, Skukuza, South Africa) from a parked field vehicle at 10–30 m with a combination of ketamine (0.2 mg/kg) and medetomidine (0.03 mg/kg). Immobilized individuals were fitted with Global Positioning System (GPS) collars (Vectronic Aerospace GmbH, Berlin, Germany) before reversal with atipamezole (0.33 mg/kg). Following reversal, individuals were observed until they rejoined other pride members. Once per week between March 2014 and December 2015, we used hand-held telemetry receivers (R-1000, Communication Specialists, Orange, California, USA) to download location data via UHF bidirectional radio link.

GPS collars were programmed to record locations every hour between 18:00 and 07:00 (when lions are most active; Ng'weno 2017, Oriol-Cotterill et al. 2015) plus a fix at 12:00; thus, all collars made 15 daily fix attempts during the study period. Outside Laikipia, lions may exhibit fission–fusion dynamics (Mosser and Packer 2009); within Laikipia (Oriol-Cotterill et al. 2015) and elsewhere (Schaller 1972), lions live in stable social units (prides) that usually hunt together. We equated activity of telemetered individuals with the probability of encountering lions from the perspective of their ungulate prey, although fusion or fission of individuals may compromise the validity of this assumption. However, for the purposes of our study, we consider this assumption reasonable for two reasons. First, we calculated overlap of telemetered individuals in the wet and dry seasons, in core areas (50% kernel) and entire home ranges (90% kernel) using a smoothing factor of 1,000 m between kernel densities and seasons. Core areas of individuals barely overlapped during both seasons (Appendix S2: Table S2; see also Mosser and Packer 2009, VanderWaal et al. 2009), and individuals exhibited minimal overlap of entire home ranges during both seasons (Appendix S2: Table S2). Second, during data downloads, we occasionally tallied the other (uncollared) members of prides that were within 100 m of the collared individual; the majority (~80%) of uncollared members of prides were within 100 m of the collared individual for >95% of data downloads. Therefore, collars permitted us to simultaneously locate kills made by specific prides and to estimate activity of specific prides. Collectively, these five prides represented 79% of the lion population at Ol Pejeta Conservancy.

We located lion kills by identifying GPS clusters using an algorithm adapted from Knopff et al. (2009; see also O'Brien et al. 2018). We defined a cluster as two or more successive GPS relocations occurring within 100 m of each other between 18:00 and 07:00 (i.e., omitting the location at 12:00). From previous work on hunting behavior of lions (Tambling et al. 2010), we assumed that clusters were indicative either of ambush locations or kill sites (collectively, "potential kill sites"). We visited potential kill sites within 3–4 d of downloading location data and searched for evidence of kills within a 50-m radius from the cluster centroid for a maximum of

30 min. Based on lion claw and bite marks on carcasses, and lion tracks, scat, and hair, we classified potential kill sites as kill sites (i.e., instances in which carcasses both were found and were verified to be killed by lions; $n = 246$), or non-kills (i.e., instances in which no carcasses were found [$n = 99$] at potential kill sites, or in which sign of other large carnivores occurred, such that we could not distinguish lion kills from scavenging by lions [$n = 23$]).

To quantify predator–prey encounters, we used GPS tracking to estimate a lion's utilization distribution (UD), which we equated with a pride's UD. We assumed that UDs represented the probability of an encounter between a lion and potential prey. We constructed 246 kill-site-specific UDs, each from the location data from a single month prior to the date at which a kill occurred, for the pride responsible for the kill. We then used kernel density estimation with least squares cross validation and a smoothing factor of 1,000 m using R package adehabitatHR version 1.8.18 (Seaman and Powell 1996, Calenge 2006).

Densities, resource selection, and predation risk for lion prey

We estimated population density (individuals/km^2) for the five species of ungulates killed frequently by lions (Appendix S1: Fig. S1) and for which we detected ≥ 20 kill sites. Collectively, these five species (hereafter "lion prey") accounted for 94% of the lion kills that we detected from GPS clusters. To quantify prey neighborhoods, we conducted a series of quarterly, vehicle-based, drive transects between August 2014 and November 2015 ($n = 6$ sampling periods). We systematically drove 12 (4–13 km) transects at 10–15 km/h, based on a predetermined, random, starting point within the study area. The same 12 transects were driven each quarter; a total of 3 d were dedicated to each sampling period. All counts were conducted between 07:00 and 11:00 by three trained observers. One observer was responsible for driving and maintaining the route via GPS, while the other two observers recorded species, herd size, sighting distance, and bearing to all lion prey. We measured sighting distance using laser rangefinders and recorded bearings using a compass. We estimated densities and effective strip width (ESW) for detection functions for each species of lion prey in each survey using the R package distance, version 0.9.7 (Miller 2017).

Using the following procedure, we generated spatially explicit density estimates for each of the five species of lion prey from each of the six surveys using resource selection functions (RSFs). First, we compared used points where lion prey were sighted during the quarterly drive transects to "available points." Available points were constrained to the distance at which ≤95% of sightings occurred from transects, specific to the species of lion prey and survey. Second, we used generalized linear mixed-effect models to estimate species × survey-specific RSF coefficients. We tested for selection of three continuous variables known to influence the abundance and distribution of lion prey on the landscape: (1) NDVI (normalized difference vegetation index, a metric associated with visibility, see Resource selection functions for kill sites); (2) distance to glades (nutrient-rich grazing lawns derived from livestock corrals [Augustine et al. 2003, Porensky and Veblen 2015,]); and (3) distance to water sources (Valeix et al. 2009*b*). Further, because the abundance and distribution of lion prey can change seasonally (e.g., Ogutu et al. 2008, Kiffner et al. 2014), we evaluated differences in selection between wet (March–May, August–November) and dry (June–July, December–February) season sampling. Transect was included in models as a random effect. We used Akaike's information criterion corrected for small sample sizes (AIC$_c$) to evaluate support for competing RSF models, then averaged parameter estimates for all models for a species with $\Delta\text{AIC}_c \leq 2$ (Burnham and Anderson 2002). We performed model selection and averaging using the R package MuMIn version 1.15.6. (Barton 2016). Then, we projected the RSF in each 30 × 30 m grid cell across our study area. We rescaled each RSF to create continuous estimates ranging between 0 (strongest avoidance) and 1 (strongest selection), which we split into five bins of equal width following Morris et al. (2016). Finally, we combined species × survey-specific densities with species × survey-specific RSFs to create spatially explicit density estimates for each species of lion prey at each survey. We validated RSF-generated estimates of prey density using camera-trap surveys (Appendix S3). For similar approaches to estimating population densities from RSFs, see Boyce et al. (2016).

From species × survey-specific densities and kill sites, we calculated Jacobs' index (D) for the five species of lion prey, where $D = (r - p)/(r + p - 2rp)$, where r is the proportion of kill sites comprised of a particular species of lion prey and p is the proportional availability of that species of lion prey (Jacobs 1974). In addition to their numerical dominance (Georgiadis et al. 2007) and high prevalence in lion diets (see below), zebra were killed in proportion to their abundance in both wet and dry seasons (Fig. 1), bolstering the interpretation that an abundant zebra population has fueled the recolonization of lions to Laikipia.

Resource selection functions for kill sites

We measured visibility as a surrogate for prey catchability. Visibility is associated inversely with predation risk for lions elsewhere in sub-Saharan Africa (Hopcraft et al. 2005, Thaker et al. 2011, Valeix et al. 2011; see also Ford et al. 2014, Riginos 2015). To measure visibility, we used the normalized difference vegetation index (NDVI) from a Rapideye satellite image (5 m resolution; Digital Globe, Longmont, Colorado, USA) acquired in May 2013 (Pettorelli et al. 2005, Bro-Jørgensen et al. 2008). We validated the relationship between NDVI and

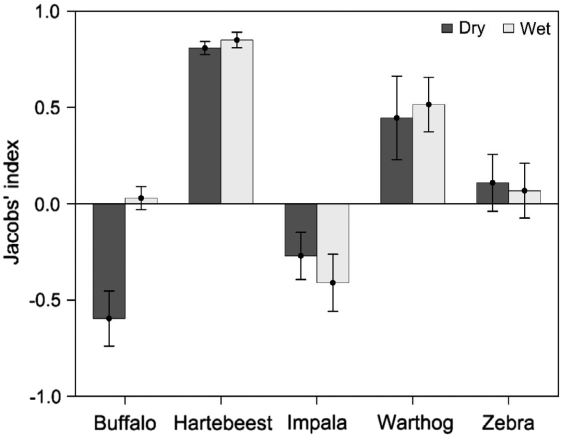

FIG. 1. Jacobs' index for selectivity of five species of lion prey (mean ± SE). Values close to 0 indicate that particular species are being killed in proportion to their availability.

visibility with the following procedure. First, we created circular plots with radii of 50 m around each of the 246 kill sites. At the center of each circular plot, we used a laser rangefinder to measure distance to the nearest obstruction (branches, leaves, thick grass) at a height of 96 cm (average shoulder height for lions) at 72° intervals (Ford et al. 2014). For each kill site, we averaged the five visibility measurements and correlated this value to the NDVI value at the center of each circular plot. Average visibility and NDVI were correlated negatively (Pearson's $r = -0.42$; $P < 0.01$), demonstrating that satellite-derived estimates of NDVI are reflective of actual visibility. We constructed kill occurrence RSFs (sensu Kauffman et al. 2007, Ford et al. 2014, Ali et al. 2017) for each species of lion prey. Kill occurrence RSFs quantify the risk of mortality from lion predation as a function of five predictor variables, framed as non-mutually exclusive hypotheses: conspecific density, total prey density, zebra density, visibility, and lion activity (Table 1).

To create kill occurrence RSFs, we employed a use-availability design (Manly et al. 2002). First, we defined "use" as kill-site locations within pride home ranges (95% UD) and defined "availability" as random points within pride home ranges, subject to the constraint that random points could not fall within 500 m of used points (Thaker et al. 2011, 2011, Gervasi et al. 2013). For each used location, we generated five available locations using GIS software (ArcGIS Version 10; ESRI 2011). For kill sites that occurred at least one week before or after the timing of our drive transects ($n = 235$ out of 246 kill sites), we computed weighted averages for pairs of species × survey-specific density estimates associated with each kill (30 × 30 m cells). For each pair of drive transects associated with these 235 kill sites, we allocated proportionally more weight to the density estimates coinciding more closely with the date at which a kill occurred. We then extracted corresponding estimates based on weighted averages of lion-prey density for each used or available location. We validated weighted averages of prey density using camera-trap surveys (Appendix S3). Then, we developed generalized linear models to represent Hypotheses 1–3, calculated $\mathrm{AIC_c}$ values and $\mathrm{AIC_c}$ weights (W_i) using the R package MumIn version 1.15.6 (Barton 2016), and used these as metrics for strength of evidence to compare the performance of competing models (Burnham and Anderson 2002). Finally, we averaged species-specific estimates of parameters in models with $\Delta\mathrm{AIC_c} \leq 2$.

Because associations between zebra density and kill occurrence of (non-zebra) focal species could arise due simply to habitat overlap, we tested this null hypothesis for focal species exhibiting a neighborhood effect with zebra (Appendix S4). All analyses were undertaken in R version 3.4.0 (R Development Core Team, 2017).

TABLE 1. Summary of hypotheses and predictor variables used to evaluate drivers of kill site occurrence.

Hypothesis		Predictor variables
Number	Description	
H1A	Prey Neighborhoods: conspecific density	conspecific density (individuals/km^2; i.e., estimated density of a focal species of lion prey) in 30 × 30 m cells
H1B	Prey Neighborhoods: total prey density	total density of prey (individuals/km^2) in 30 × 30 m cells
H1C	Prey Neighborhoods: zebra density	zebra density (individuals/km^2) in 30 × 30 m cells
H2	Prey Catchability	visibility (i.e., 1 − NDVI) in 30 × 30 m cells
H3	Predator–Prey Encounters	lion activity (95% utilization distribution) in 30 × 30 m cells
H1 × H2	Prey Neighborhoods × Prey Catchability (submodels A–C)	interaction between individual terms for prey neighborhoods and visibility
H1 × H3	Prey Neighborhoods × Predator–Prey Encounters (submodels A–C)	interaction between individual terms for prey neighborhoods and lion activity
H2 × H3	Prey Catchability × Predator–Prey Encounters	interaction between visibility and lion activity
H1 × H2 × H3	Prey Neighborhoods × Prey Catchability × Predator–Prey Encounters (submodels a–c)	interaction between individual terms for prey neighborhoods, visibility, and lion activity

Notes: The Prey Neighborhoods Hypothesis includes three submodels (A–C), each of which was tested interactively with the Prey Catchability and Predator–Prey Encounters Hypotheses.

Results

We recorded 17,788 GPS relocations from collared lionesses (average 4,447 ± 31 locations per individual [mean ± SE]). Average home range size for prides during the wet season (March–May, August–November) averaged 79.3 ± 18.3 km^2, while dry season (December–February, June–July) home ranges averaged 69.4 ± 20.1 km^2. From August 2014 to December 2015, we located 246 kill sites of which 231 were the aforementioned five species of lion prey (Appendix S5: Table S1).

For no species of lion prey did season influence resource selection (Appendix S6: Table S1), so we did not generate kill occurrence RSFs for separate seasons. Prey neighborhoods predicted kill occurrences for buffalo, hartebeest, and warthogs, although the null (intercept only) model was within 2 AIC units of the top-supported model for warthogs. Conspecific density did not predict kill occurrence for any species of lion prey (Table 2). Buffalo were killed less frequently (Table 2; Fig. 2a, Fig. 3a) and hartebeest were killed more frequently (Table 2; Fig. 2b, Fig. 3b) with increasing zebra density; we rejected the null hypothesis that these neighborhood effects were due simply to habitat overlap between zebra and hartebeest (Appendix S4: Fig. S1a) or lack thereof between zebra and buffalo (Appendix S4: Fig. S1b). For buffalo, the neighborhood effect with zebra was more pronounced where lions were most active. Hartebeest were killed less frequently with increasing visibility and lion activity (Fig. 2b, Fig. 3b).

Interactions between prey neighborhoods, visibility, and lion activity predicted kill occurrence for every species of lion prey but warthog, although model fit was poor for impala (Table 2; Fig. 2c); no three-way interaction was supported for any species of lion prey (Table 2). The probability of occurrence for buffalo kill sites decreased with increasing zebra density where lions were most active, but showed no relationships with zebra density where lion activity was minimal (Fig. 2a; Fig 3a). Hartebeest were killed more frequently where visibility was high at maximal lion activity, and were killed more frequently where visibility was low at minimal lion activity (Fig. 2b; Fig. 3b). For zebra, risk of predation declined gradually with increasing visibility in areas of high lion activity; in areas where lion activity was low, kill occurrence for zebra decreased steeply with increasing visibility (Fig. 2d; Fig. 3c).

Discussion

For four of the five species of lion prey in our system, we found support for a combination of prey neighborhoods, prey catchability, and predator–prey encounters in driving landscape-level patterns of kill site occurrence. Prey neighborhoods altered risk of predation for individuals of at least two of the five focal species of lion prey (buffalo and hartebeest), via distinct pathways. Buffalo experienced lower predation risk when associating with zebra when encounters with lions were frequent, supporting the hypothesis that prey neighborhoods dilute risk for some species (Sinclair 1985, Fitzgibbon 1990, Mathis and Chivers 2003, Stensland et al. 2003, Schmitt et al. 2014, Sutton et al. 2015). On the other hand, predation risk for hartebeest was elevated in association with zebra, implying that apparent competition with zebra may negatively impact hartebeest populations (Ng’weno et al. 2017; see also James et al. 2004, DeCesare et al. 2010, Wittmer et al. 2013). Because lions have been restored to Laikipia relatively recently (Georgiadis

Table 2. Results of model selection (ΔAIC_c) for hypotheses on species-specific resource selection functions for kill occurrence.

Hypothesis		Buffalo	Hartebeest	Impala	Warthog	Zebra
Number	Null Model (intercept only)	3.62	5.03	4.18	1.57	45.33
H1A	Prey Neighborhoods: conspecific density	4.77	3.06	6.22	3.27	47.34
H1B	Prey Neighborhoods: total prey density	4.78	4.92	5.42	1.74	47.32
H1C	Prey Neighborhoods: zebra density	0.82	1.51	6.20	3.26	-
H2	NDVI	5.56	0.00	4.55	0.00	32.92
H3	Lion Activity	1.74	6.34	0.00	3.55	20.92
H1A × H2	Conspecific Density × NDVI	8.84	2.84	7.86	2.13	35.45
H1A × H3	Conspecific Density × Lion Activity	4.85	6.30	4.11	7.25	24.67
H1B × H2	Total Prey Density × NDVI	8.00	2.64	8.45	2.29	35.95
H1B × H3	Total Prey Density × Lion Activity	3.30	7.81	2.04	4.69	23.77
H1C × H2	Zebra Density × NDVI	4.64	2.07	8.36	3.21	-
H1C × H3	Zebra Density × Lion Activity	0.00	4.77	3.60	7.22	-
H2 × H3	NDVI × Lion Activity	5.52	0.83	1.54	3.66	0.00
H1A × H2 × H3	Conspecific Density × NDVI × Lion Activity	13.06	7.53	5.13	9.80	5.65
H1B × H2 × H3	Total Prey Density × NDVI × Lion Activity	10.51	7.38	4.84	9.06	6.51
H1C × H2 × H3	Zebra Density × NDVI × Lion Activity	8.05	5.51	2.09	9.64	-

Notes: NDVI, normalized difference vegetation index. Boldface type indicates the change in the Akaike information criterion corrected for sample size (ΔAIC_c). Models are depicted graphically in Fig. 2. For zebra, models containing “zebra density” are redundant with those containing “conspecific density.”

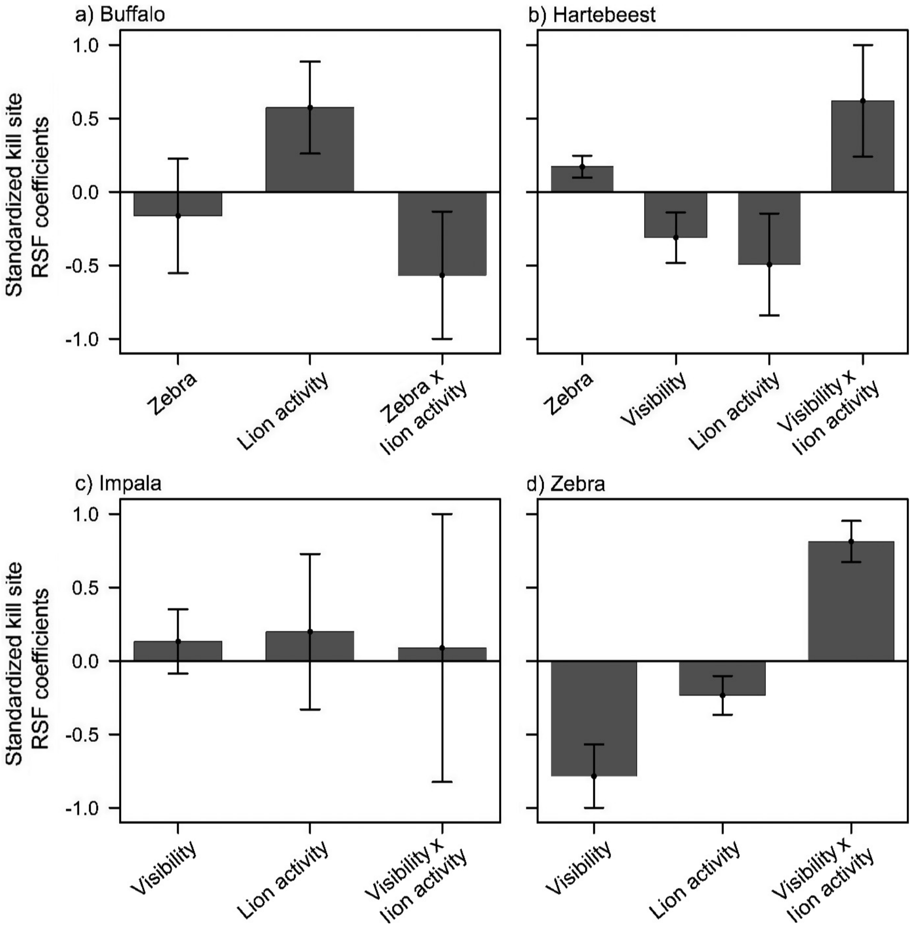

FIG. 2. Standardized coefficients (β ± SEM) from kill-site resource selection functions with the strongest support for (a) buffalo, (b) hartebeest, (c) impala, and (d) zebra. Bars appear for main effects and interaction terms included in the supported models. Error bars represent standard errors. A positive coefficient for lion activity indicates higher risk of predation when and where lion utilization is high. A positive coefficient for visibility indicates higher risk of predation in the open (i.e., where NDVI is low) and vice versa.

et al. 2007, Ng'weno et al. 2017), associations between zebra and hartebeest may be transitory and are likely to become less common in the future. Our work provides a complementary approach to a series of studies (Kauffman et al. 2007, Valeix et al. 2009*b*, Anderson et al. 2010, 2016, Thaker et al. 2011, Creel et al. 2014, Ford et al. 2014, Gallagher et al. 2017, O'Brien et al. 2018) that attribute spatial variation in predation risk to variation in catchability, predator–prey encounters, or both (Fig. 3). We add to this work with the discovery that spatial variation in prey neighborhood structure can either amplify or dilute the risk of predation experienced by individuals (Fig. 4).

In addition to the influence of prey neighborhoods on kill site occurrence, our work supports the influence of prey catchability and predator–prey encounters in driving landscape-level patterns of predation, as has been described elsewhere (Hopcraft et al. 2005, Thaker et al. 2011, Valeix et al. 2011, Loarie et al. 2013, Ford et al. 2014). The majority of prey species incurred higher mortality in areas where lion activity was high. Where lion activity was low, kills of hartebeest and zebra were unlikely in all but the most densely vegetated areas characterized by low visibility. Where lion activity was high, occurrence of zebra kills declined steadily with increasing visibility, whereas occurrence of hartebeest kills increased with increasing visibility. This result suggests that changes in visibility (e.g., via shrub encroachment or bush clearing [Ford et al. 2016,]) in combination with shifting patterns of lion extirpation and restoration (Georgiadis et al. 2007, Bauer et al. 2015, Ng'weno et al. 2017) will differentially alter the abundance and distribution of lion prey. Given that hartebeest are of strong conservation concern in Laikipia (Georgiadis et al. 2007), efforts to spatially segregate lions and hartebeest in open habitats are likely to improve survival rates of hartebeest.

The degree to which prey neighborhoods dilute or exacerbate risk should depend on predator selection for a focal species relative to those in its neighborhood.

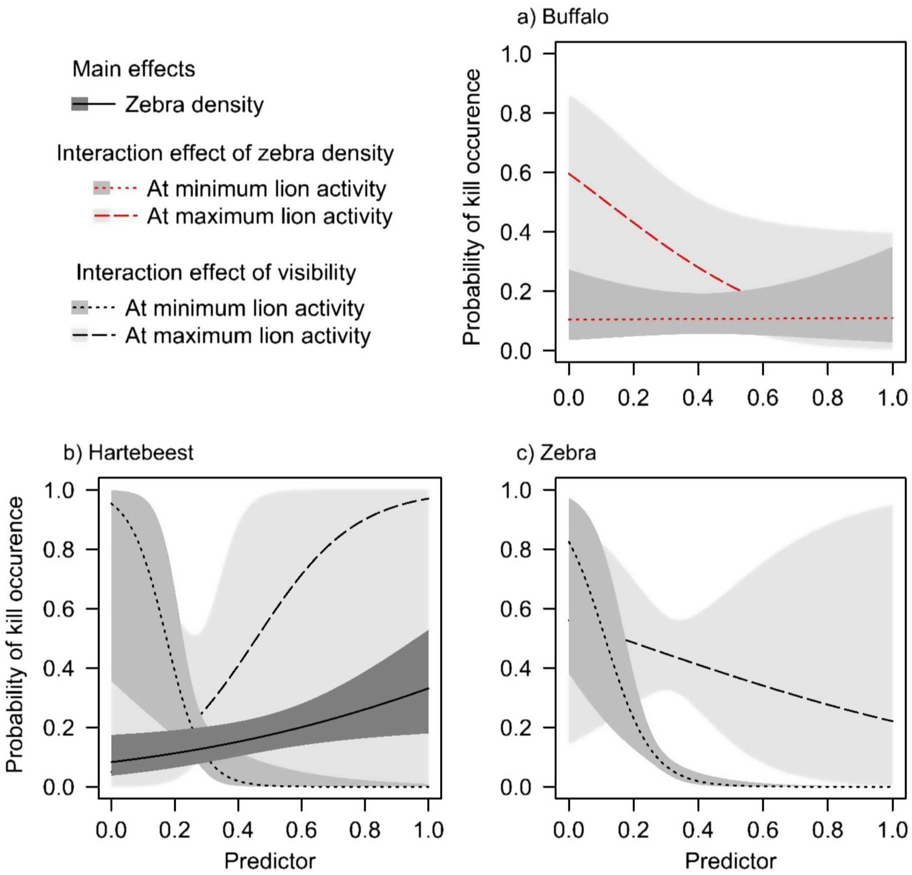

FIG. 3. Graphical predictions and 90% confidence intervals from kill-site resource selection functions for three species of lion prey. The effect of visibility on the predicted probability of kill occurrence differs across levels of lion utilization and vice versa, i.e., probability of kill occurrence changes with one-unit change of zebra density and visibility while holding lion utilization constant at different levels (minimum = 0.05 and maximum = 0.95).

Across their geographic range, lions prefer prey with a mean mass of ca. 200 kg (Hayward and Kerley 2005); at our study site, however, lions selected for hartebeest (~100 kg), killed zebra (~175 kg) in proportion to their abundance (see also O'Brien et al. 2018) and avoided prey toward the opposite ends of the size spectrum (impala [~30 kg], buffalo [~400 kg]). Consequently, association with zebra exacerbated risk of predation to hartebeest and diluted risk for buffalo. Despite their small size, we speculate that warthogs are selected due to some combination of slow evasion speeds and reduced vigilance, relative to other lion prey (see also Hayward and Kerley 2005).

Neighborhood effects should be widespread in multi-prey systems where species differ in their vulnerability to predation, and are expected to occur through at least two pathways. First, neighborhood effects may emerge when predators concentrate hunting in areas of high abundance for their primary (i.e., most commonly consumed) prey, and consume other (less commonly consumed, secondary) prey by virtue of their proximity to primary prey. Such short-term apparent competition (i.e., "associational susceptibility" [White and Whitham 2000,] or "shared doom" [Wahl and Hay 1995]) characterized prey neighborhoods of hartebeest, which incurred higher risk of predation in association with zebra. Second, and conversely, association with a diversity of prey may divert predators from consuming particular species, thereby reducing predation on that species (Whelan et al. 2003, Hughes 2012). Such an associational refuge conferred safety to buffalo in association with zebra where lions were most active (Fig. 3a). In the presence of alternative prey, buffalo likely are a more dangerous option for lions, and may therefore be avoided (Mukherjee and Heithaus 2013).

A major challenge for future study is to understand the scale dependence over which prey neighborhoods are perceived by predators, as scale-dependent neighborhood effects have been noted elsewhere (e.g., Emerson et al. 2012, Champagne et al. 2016). In other words, over what temporal and spatial extents do individuals experience costs or benefits of prey neighborhoods? Elsewhere in sub-Saharan Africa, ungulates aggregate more strongly in the dry season. In such instances, we

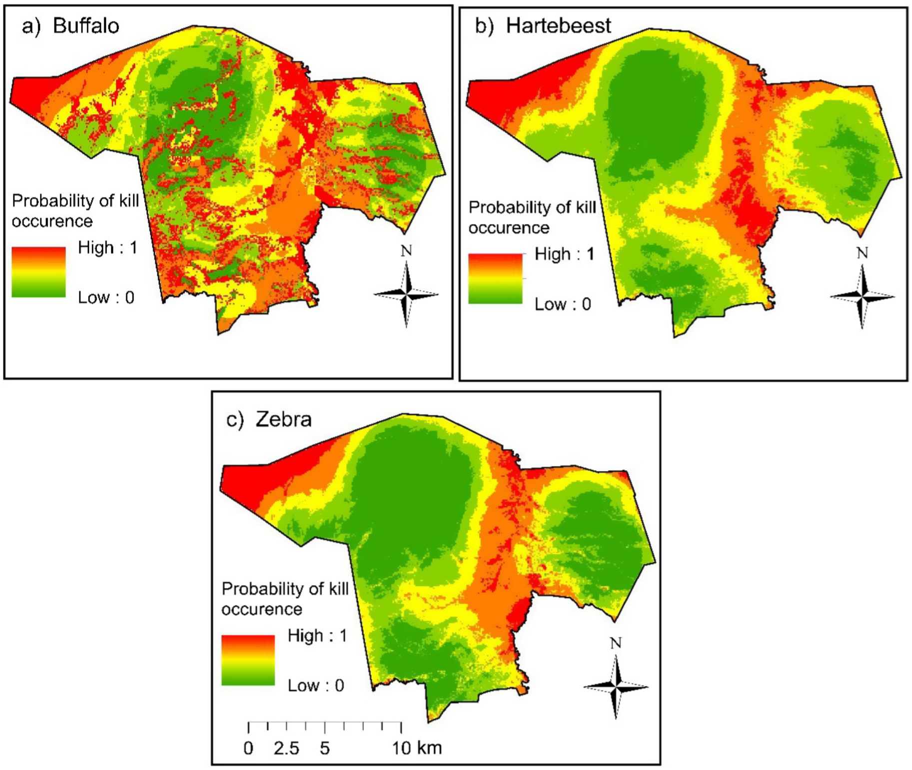

Fig. 4. Spatial variation in risk of predation based on model-averaged coefficients from resource selection functions of kill occurrence for (a) buffalo, (b) hartebeest, and (c) zebra. The boundary for Ol Pejeta Conservancy boundary is shown as a thick black line. Predation risk transitions from high (red) to low (green) risk.

might expect the effects of prey neighborhoods, positive or negative, to be accentuated, as individuals congregate around water sources and other limited resources (Ayeni 1975, Valeix 2011). Ultimately, our inferences are constrained by the fact that bulk of our sampling was conducted during the wet season, with only one set of drive transects conducted in the dry season. In light of the fact that ungulates tend to be dispersed widely in the wet season, we believe our results are conservative: given more extensive data during the dry season, we expect the influence of prey neighborhoods on kill-site occurrence might have been magnified.

With regard to spatial scale, we restricted prey neighborhoods to 900-m^2 grid cells, which we selected as a compromise between the size of pride home ranges, the number of grid cells in which kill sites occurred, and the area over which prey aggregations arose. This spatial scale was sufficiently resolute to detect neighborhood effects for two of the five species of lion prey in our system. In a recent meta-analysis of plant–herbivore interactions, decreasing spatial scale (plot size) increased the strength of neighborhood effects, regardless of the direction of the effect (Champagne et al. 2016). We cannot rule out the possibility that, had we attempted to quantify prey neighborhoods at spatial scales finer than 900 m^2, we would have detected neighborhood effects in risk of mortality for the remaining species of lion prey (i.e., impala, warthog, and zebra, in addition to buffalo and hartebeest). At least with respect to predation by lions per se, we believe this scenario to be unlikely for two reasons. First, predation on impala is distributed relatively evenly among lions, leopards, and cheetahs (Appendix S1: Fig. S1), and impala are rarely targeted by lions elsewhere (Hayward and Kerley 2005, Ford et al. 2014, Davies et al. 2016). Therefore, while impala may confer increased vigilance and early detection in prey neighborhoods, their own mortality likely is less sensitive to predation by lions than more commonly consumed ungulates. Second, zebra are at least twice as abundant as buffalo, warthog, and hartebeest at Ol Pejeta (Appendix S5: Table S1), and therefore should be particularly influential with regard to consumption of rarer (secondary) prey (see also Root 1973).

Although they exhibit a rich intellectual history in the study of plant–herbivore interactions (e.g., Root 1973, Callaway 1995, Brooker et al. 2008, Barbosa et al. 2009, Coverdale et al. 2018) and pest control (e.g., Root and Kareiva 1984, Kromp 1999, Landis et al. 2000, Zehnder et al. 2007), neighborhood effects are less widely appreciated in predator–prey systems, particularly those dominated by large mammals. In conjunction with classic components of predation (predator–prey encounter rates and catchability), we have demonstrated the importance of prey neighborhoods in influencing risk of predation in a multi-prey, single predator savanna ecosystem. We encourage ecologists working on predator–prey interactions in multi-prey systems to consider the potential for prey neighborhoods to shape risk of predation across expansive landscapes, and to develop studies to quantify whether and how prey deliberately form neighborhoods.

ACKNOWLEDGMENTS

C. C. Ng'weno, A. T. Ford, and J. R. Goheen designed the research; C. C. Ng'weno, A. K. Kibungei, and J. R. Goheen collected the field data; C. C. Ng'weno and A. K. Kibungei analyzed the data; C. C. Ng'weno, A. T. Ford, and J. R. Goheen wrote the manuscript, all authors edited the manuscript. We thank Earthwatch volunteers (2013–2015) and undergraduate students from various universities in Kenya who collected supported on data collection over the years. C. Bopp, P. Kimaita, D. Kamaru, and N. Ndiema provided expert assistance in the field. J. Alston, B. Brito, S. Buskirk, J. Beck, S. Esmaeili, K. Gerow, M. Hayward, B. Jesmer, M. Kauffman, B. Maitland, N. Owen-Smith, and an anonymous reviewer provided helpful comments on the manuscript. B. Gituku, S. Mutisya, and the Ecological Monitoring Unit facilitated fieldwork and logistical support at Ol Pejeta Conservancy. Funding was provided by Schlumberger Foundation Faculty for the Future, the Earthwatch Institute, Conservation, Research and Education Opportunities International, the Russell E. Train fellowship program of the World Wildlife Fund, the Biodiversity Institute of the University of Wyoming, and the Haub School of Environment and Natural Resources of the University of Wyoming.

LITERATURE CITED

Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49:340–346.

Ali, A. T., A. Ford, J. Evans, D. Mallon, M. Hayes, J. King, R. Amin, and J. R. Goheen. 2017. Resource selection and landscape change reveal mechanisms suppressing population recovery for the world's most endangered antelope. Journal of Applied Ecology 54:1720–1729.

Anderson, T. M., J. G. C. Hopcraft, S. Eby, M. Ritchie, J. B. Grace, and H. Olff. 2010. Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. Ecology 91:1519–1529.

Anderson, T. M., S. White, B. Davis, R. Erhardt, M. Palmer, A. Swanson, M. Kosmala, and C. Packer. 2016. The spatial distribution of African savannah herbivores: species associations and habitat occupancy in a landscape context. Philosophical Transactions of the Royal Society B 371:20150314.

Atwood, T. C., E. M. Gese, and K. Kunkel. 2009. Spatial partitioning of predation risk in a multiple predator-multiple prey system. Journal of Wildlife Management 73: 876–884.

Augustine, D. J., S. J. McNaughton, and D. A. Frank. 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. Ecological Applications 13:1325–1337.

Ayeni, J. S. O. 1975. Utilization of waterholes in Tsavo National Park (East). African Journal of Ecology 13:305–323.

Barbosa, P., J. Hines, I. Kaplan, H. Martinson, A. Szczepaniec, and Z. Szendrei. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. Annual Review of Ecology Evolution and Systematics 40:1–20.

Barton, K. 2016. MuMIn: Multi-Model Inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn

Bauer, H., G. Chapron, K. Nowell, P. Henschel, P. Funston, L. T. Hunter, D. W. MacDonald, and C. Packer. 2015. Lion populations are declining rapidly across Africa, except in intensively managed areas. Proceedings of the National Academy of Sciences USA 112:14894–14899.

Bertram, B. C. R. 1978. Living in groups: predators and prey. Pages 64–96 *in* J. R. Krebs, and N. B. Davies, editors. Behavioural ecology. Blackwell Scientific Press, Oxford, UK.

Birkett, A. 2002. The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. African Journal of Ecology 40:276–282.

Boyce, M. S., C. J. Johnson, E. H. Merrill, S. E. Nielsen, E. J. Solberg, and B. van Moorter. 2016. Can habitat selection predict abundance? Journal of Animal Ecology 85:11–20.

Breviglieri, C. P. B., P. S. Oliveira, and G. Q. Romero. 2017. Fear mediates trophic cascades: non-consumptive effects of predators drive aquatic ecosystem function. American Naturalist 189:490–500.

Bro-Jørgensen, J., M. E. Brown, and N. Pettorelli. 2008. Using the satellite-derived normalized difference vegetation index (NDVI) to explain ranging patterns in a lek-breeding antelope: the importance of scale. Oecologia 158: 177–182.

Brooker, R. W., et al. 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology 96:18–34.

Brown, J. S., and W. A. Mitchell. 1989. Diet selection on depletable resources. Oikos 54:33–43.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Callaway, R. M. 1995. Positive interactions among plants. Botanical Review 61:306–349.

Caro, T., and S. Girling. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, Illinois, USA.

Champagne, E., J. Tremblay, and S. Côté. 2016. Spatial extent of neighboring plants influences the strength of associational effects on mammal herbivory. Ecosphere 7:e01371.

Coverdale, T. C., J. R. Goheen, T. M. Palmer, and R. M. Pringle. 2018. Good neighbors make good defenses: associational refuges reduce defense investment in African savanna plants. Ecology 99:1724–1736.

Craft, M. E. 2015. Infectious disease transmission and contact networks in wildlife and livestock. Philosophical Transactions of the Royal Society B 370:20140107.

Creel, S., P. Schuette, and D. Christianson. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behavioral Ecology 25:773–784.

Davies, A., C. J. Tambling, G. Kerley, and G. Asner. 2016. Limited spatial response to direct predation risk by African herbivores following predator reintroduction. Ecology and Evolution 6:5728–5748.

DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. Animal Conservation 13:353–362.

Dehn, M. M. 1990. Vigilance for predators: detection and dilution effects. Behavioral Ecology and Sociobiology 26:337–342.

Emerson, S. E., J. S. Brown, C. J. Whelan, and K. A. Schmidt. 2012. Scale-dependent neighborhood effects: shared doom and associational refuge. Oecologia 168:659–670.

ESRI. 2011. ArcGIS desktop: release 10. Environmental Systems Research Institute, Redlands, California, USA.

Fischhoff, I. R., S. R. Sundaresan, J. Cordingley, and D. I. Rubenstein. 2007. Habitat use and movements of plains zebra in response to predation danger from lions. Behavioral Ecology 18:726–729.

Fitzgibbon, C. 1990. Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. Animal Behavior 39:1116–1126.

Ford, A. T., J. R. Goheen, T. O. Otieno, L. Bidner, L. A. Isbell, T. M. Palmer, D. Ward, R. Woodroffe, and R. M. Pringle. 2014. Large carnivores make savanna tree communities less thorny. Science 346:346–349.

Ford, A. T., J. M. Fryxell, and A. R. E. Sinclair. 2016. Conservation challenges facing African savanna ecosystems. Antelope conservation: from diagnosis to action. Wiley-Blackwell, Hoboken, New Jersey, USA.

Fortin, D., and M. E. Fortin. 2009. Group-size-dependent association between food profitability, predation risk and distribution of free-ranging bison. Animal Behavior 78:887–892.

Frank, L. G., D. Simpson, and R. Woodroffe. 2003. Foot snares: an effective method for capturing African lions. Wildlife Society Bulletin 31:309–314.

Gallagher, A., S. Creel, R. P. Wilson, and S. J. Cooke. 2017. Energy landscapes and the landscape of fear. Trends in Ecology & Evolution 32:88–96.

Georgiadis, N. J., J. G. N. Olwero, G. Ojwang', and S. S. Romañach. 2007. Savanna herbivore dynamics in a livestock-dominated landscape: I. dependence on land use, rainfall, density, and time. Biological Conservation 137:461–472.

Gervasi, V., H. Sand, B. Zimmermann, J. Mattisson, P. Wabakken, and J. Linnell. 2013. Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. Ecological Applications 23:1722–1734.

Goodale, E., G. Beauchamp, and G. D. Ruxton. 2017. Mixed-species groups of animals: behavior, community structure, and conservation. Academic Press, Cambridge, Massachusetts, USA.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295–311.

Hawlena, D., and O. J. Schmitz. 2010. Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. Proceedings of the National Academy of Sciences USA 107:15503–15507.

Hayward, M. W., and G. I. H. Kerley. 2005. Prey preferences of the lion (*Panthera leo*). Journal of Zoology 267:309–322.

Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. Oikos 111:101–111.

Holt, R. D., and B. P. Kotler. 1987. Short-term apparent competition. American Naturalist 130:412–430.

Hopcraft, J. G., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74:559–566.

Hopcraft, J. G., H. Olff, and A. R. E. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends in Ecology & Evolution 25:119–128.

Hughes, A. R. 2012. A neighboring plant species creates associational refuge for consumer and host. Ecology 93:1411–1420.

Hunter, L., and J. D. Skinner. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour 135:195–211.

Jacobs, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. Oecologia 14:413–417.

James, A. R. C., S. Boutin, D. M. Hebert, and A. B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management 68:799–809.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator prey system. Ecology Letters 10:690–700.

Kiffner, C., J. Kioko, C. Leweri, and S. Krause. 2014. Seasonal patterns of mixed species groups in large East African mammals. PLoS ONE 9:e113446.

Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management 73:586–597.

Krause, J., and G. D. Ruxton. 2002. Living in groups. Oxford University Press, New York, New York, USA.

Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. Agriculture, Ecosystems & Environment 74:187–228.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology 45:175–201.

Lehtonen, J., and K. Jaatinen. 2016. Safety in numbers: the dilution effect and other drivers of group life in the face of danger. Behavioral Ecology and Sociobiology 70:449–458.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Loarie, S., C. J. Tambling, and G. Asner. 2013. Lion hunting behaviour and vegetation structure in an African savanna. Animal Behavior 85:899–906.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Wallace. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordrecht, Netherlands.

Mathis, A., and P. Chivers. 2003. Overriding the oddity effect in mixed-species aggregations: group choice by armored and nonarmored prey. Behavioral Ecology 14:334–339.

Miller, D. L. 2017. Distance sampling detection function and abundance estimation. R package version 0.9.7. https://CRAN.R-project.org/package=Distance

Moll, R. J., K. M. Redilla, T. Mudumba, A. B. Muneza, S. M. Gray, L. Abade, M. W. Hayward, J. J. Milspaugh, and R. A. Montgomery. 2017. The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. Journal of Animal Ecology 86:749–765.

Morris, T., and M. Letnic. 2017. Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. Proceedings of the Royal Society B 284:20170111.

Morris, L. M., K. M. Proffitt, and J. K. Blackburn. 2016. Mapping resource selection functions in wildlife studies: concerns and recommendations. Applied Geography 76:173–183.

Mosser, A., and C. Packer. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. Animal Behavior 78:359–370.

Mukherjee, S., and M. R. Heithaus. 2013. Dangerous prey and daring predators: a review. Biological Reviews 88:550–563.

Ng’weno, C. C. 2017. Predator-prey interactions and apparent competition following the restoration of lions to a human-occupied savanna. Dissertation. University of Wyoming, Laramie, Wyoming.

Ng’weno, C. C., N. J. Maiyo, A. H. Ali, A. K. Kibungei, and J. Goheen. 2017. Lions influence the decline and habitat shift of hartebeest in a semiarid savanna. Journal of Mammalogy 98:1078–1087.

O’Brien, T. G., M. F. Kinnaird, S. Ekwanga, C. Wilmers, T. Williams, A. Oriol-Cotterill, D. I. Rubenstein, and L. G. Frank. 2018. Resolving a conservation dilemma: vulnerable lions eating endangered zebras. PLoS ONE 13:e0201983.

Ogutu, J. O., H. P. Piepho, H. T. Dublin, N. Bhola, and R. S. Reid. 2008. Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. Journal of Animal Ecology 77:814–829.

Olson, R. S., A. Hintze, F. C. Dyer, D. B. Knoester, and C. Adami. 2013. Predator confusion is sufficient to evolve swarming behaviour. Journal of the Royal Society, Interface 10:20130305–20130305.

Oriol-Cotterill, A., D. W. MacDonald, M. Valeix, S. Ekwanga, and L. G. Frank. 2015. Spatio-temporal patterns of lion space use in a human-dominated landscape. Animal Behavior 101:27–39.

Owen-Smith, N., and M. Mills. 2008. Predator-prey size relationships in an African large-mammal food web. Journal of Animal Ecology 77:173–183.

Paine, R. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Peckarsky, B. L., et al. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. Ecology 89:2416–2425.

Pettorelli, N., J. O. Vik, A. Mysterud, J. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution 20:503–510.

Porensky, L. M., and K. E. Veblen. 2015. Generation of ecosystem hotspots using short-term cattle corrals in an African savanna. Rangeland Ecology and Management 68:131–141.

Preisser, E. L., and J. L. Orrock. 2012. The allometry of fear: interspecific relationships between body size and response to predation risk. Ecosphere 3:77.

Pulliam, R. H., and T. Caraco. 1984. Living in groups: Is there an optimal group size? Pages 122–147 *in* J. R. Krebs and N. B. Davies, editors. Behavioral ecology: an evolutionary approach. Second edition. Sinauer, Sunderland, Massachusetts, USA.

R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/

Riginos, C. 2015. Climate and the landscape of fear in an African savanna. Journal of Animal Ecology 84:124–133.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards, *Brassica oleracea*. Ecological Monographs 43:95–124.

Root, R. B., and P. M. Kareiva. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences and adaptive significance of Markovian movements in a patchy environment. Ecology 65:147–165.

Schaller, G. B. 1972. The Serengeti lion: a study of predator-prey relations. University of Chicago Press, Chicago, Illinois, USA.

Schmidt, K. A., J. R. Goheen, and R. Naumann. 2001. Incidental nest predation in songbirds: behavioral indicators detect ecological scales and processes. Ecology 82:2937–2947.

Schmitt, M. H., K. Stears, C. Wilmers, and A. M. Shrader. 2014. Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds. Animal Behavior 96:151–158.

Seaman, D. E., and R. A. Powell. 1996. Accuracy of kernel estimators for animal home range analysis. Ecology 77:2075–2085.

Sinclair, A. R. E. 1985. Does interspecific competition or predation shape the African ungulate community? Journal of Animal Ecology 54:899–918.

Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. Nature 425:288–290.

Sridhar, H., G. Beauchamp, and K. Shanker. 2009. Why do birds participate in mixed-species foraging flocks? a large-scale synthesis. Animal Behavior 78:337–347.

Stensland, E., A. Angerbjorn, and P. Berggren. 2003. Mixed species groups in mammals. Mammal Review 33:205–223.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.

Sutton, G., A. Hoskins, and J. Arnould. 2015. Benefits of group foraging depend on prey type in a small marine predator, the little penguin. PLoS ONE 10:e0144297.

Tambling, C. J., E. Z. Cameron, J. T. Du Toit, and W. M. Getz. 2010. Methods for locating African lion kills using global positioning system movement data. Journal of Wildlife Management 74:549–556.

Thaker, M., A. Vanak, C. Owen, M. Ogden, S. Niemann, and R. Slotow. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. Ecology 92:398–407.

Valeix, M. 2011. Temporal dynamics of dry-season water-hole use by large African herbivores in two years of contrasting rainfall in Hwange National Park, Zimbabwe. Journal of Tropical Ecology 27:163–170.

Valeix, M., A. J. Loveridge, S. Chamaillé-Jammes, Z. Davidson, F. Murindagomo, H. Fritz, and D. W. Macdonald. 2009*a*. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology 90:23–30.

Valeix, M., H. Fritz, A. J. Loveridge, Z. Davidson, J. E. Hunt, F. Murindagomo, and D. W. Macdonald. 2009*b*. Does the risk of encountering lions influence African herbivore behaviour at waterholes? Behavioral Ecology and Sociobiology 63:1483–1494.

Valeix, M., S. Chamaillé-Jammes, A. J. Loveridge, Z. Davidson, J. E. Hunt, H. Madzikanda, and D. W. Macdonald. 2011. Understanding patch departure rules for large carnivores: lion movements support a patch-disturbance hypothesis. American Naturalist 178:269–275.

VanderWaal, K. L., A. Mosser, and C. Packer. 2009. Optimal group size, dispersal decisions, and postdispersal relationships in female African lions. Animal Behavior 77:949–954.

Wahl, M., and M. E. Hay. 1995. Associational resistance and shared doom: effects of epibiosis on herbivory. Oecologia 102:329–340.

Wahungu, G. M., L. K. Mureu, D. M. Kimuyu, A. Birkett, P. G. Macharia, and J. Burton. 2011. Survival, recruitment and dynamics of *Acacia drepanolobium Sjostedt* seedlings at Ol Pejeta Conservancy, Kenya, between 1999 and 2009. African Journal of Ecology 49:227–233.

Ward, A. J. W., J. E. Herbert-Read, D. J. T. Sumpter, and J. Krause. 2011. Fast and accurate decisions through collective vigilance in fish shoals. Proceedings of the National Academy of Sciences USA 108:2312–2315.

Whelan, C. J., J. S. Brown, and G. Maina. 2003. Search biases, frequency-dependent predation. Evolutionary Ecology Research 5:329–343.

White, J. A., and T. G. Whitham. 2000. Associational susceptibility of cottonwood to a box elder herbivore. Ecology 81:1795–1803.

Wittmer, H. U., R. Serrouya, L. M. Elbroch, and A. J. Marshall. 2013. Conservation strategies for species affected by apparent competition. Conservation Biology 27:254–260.

Zehnder, G., G. M. Gurr, S. Kühne, M. R. Wade, S. D. Wratten, and E. Wyss. 2007. Arthropod pest management in organic crops. Annual Review of Entomology 52:57–80.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2698/suppinfo